THE ROLE OF SOIL FAUNA IN AGRICULTURAL SYSTEMS

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ABSTRACT

The role of soil fauna in nitrogen cycling can not simply be quantified as metabolic transfers and tissue turnover because they have a wide range of indirect effects on the soil environments for microbial populations and processes, and plant root growth and nutrient uptake. Furthermore, the hydrology of soils, and hence soil erosion and nutrient leaching from the system, are also affected by the burrowing and feeding activities of soil fauna; notably by termites and earthworms.

The scale at which the animals affect soil processes and their overall contribution to ecosystem-level processes is related to the body size and population densities of the animals. Size is of particular significance in determining whether animals directly affect microbial populations through feeding activities or indirectly influence the environments in which they operate by modifying soil physicochemical properties.

The agronomic significance of soil fauna (other than pest species) depends upon the intensity of cropping systems because grazing, fire, tillage, inorganic fertilizers and pesticides generally reduce the species complement and population densities of soil fauna, and override their contribution to soil processes. In minimum-tillage and pasture systems their effects become more evident but are sometimes difficult to separate from improvements in soil properties as a consequence of management practices.

It is concluded that in intensively cultivated systems the potential value of soil fauna in crop production may be manifested in microfaunal/ microbial activities in the rhizosphere and with decreasing intensity of management the role of macrofauna on soil structure is more significant. But the main constraint to constructing possible scenarios for manipulating soil fauna to

improve crop production is a lack of understanding of the links between gross soil processes and the structure of soil organism communities.

INTRODUCTION

The soil fauna includes a wide range of taxonomic groups from protozoa and microarthropods to moles and larger vertebrates which live and feed in soil. It is axiomatic, therefore, that they will variously affect soil physical, chemical and microbiological processes at some scale and to some degree. There is a vast literature on the role of invertebrates in soils. A wide spectrum of vertebrate and invertebrate effects is considered by Hole (1981), Zlotin and Khodashova (1980), Anderson et al. (1981, 1984) and Fitter et al. (1985), and the roles of earthworms in soils are covered by Ghilarov (1982), Satchell (1983) and Lee (1985). Despite extensive research in this field there is little quantitative information on the role of soil animals in mediating nutrient fluxes at the ecosystem level or on the agronomic importance of soil invertebrates other than earthworms and pest species.

The question addressed here is whether significant quantitative effects on crop production occur as a consequence of the presence, absence or temporal change in the activities of invertebrate populations in soils and their interactions with microorganisms involved in N cycling. Plant growth is taken as the ultimate criterion for the importance of these soil invertebrate effects because roots ramify through the soil matrix at a density necessary to optimise nutrient uptake (Robinson and Rorison 1983; Bowen 1984). Nitrogen mineralization in soil microsites is therefore integrated by plant uptake over spatial and temporal scales which may not be detectable by bulk soil measurements (Anderson 1987). Plant growth can also be indirectly influenced by invertebrates through changes in soil structure and the physical environment of roots, effects on mycorrhizas and root pathogens in the rhizosphere and the production of plant growth substances. These, and other effects of invertebrates in soils, are undoubtedly real phenomena but at what frequency or intensity must they occur for crop production to be affected? Similar considerations apply to processes affecting N losses through nitrate leaching, denitrification or removal of organic N from the system (e.g. by termites).

Soil invertebrates range in size from amoebae to giant earthworms of more than a metre in length. Even within groups the size variation may be extreme; such as differences in mass of 50,000 between the smallest and largest earthworms (Lee 1985). Population densities of macro-, meso- and micro-fauna also exhibit wide variation from a few individuals to many millions/m^2 (Fig. 1) with generation times ranging from a year to a few hours respectively. Hence the invertebrate contribution to N fluxes in soils is the sum of activities of a great diversity of organisms and their interactions over a wide range of spatial and temporal scales, and involving both direct and indirect effects of their activities which affect plant growth.
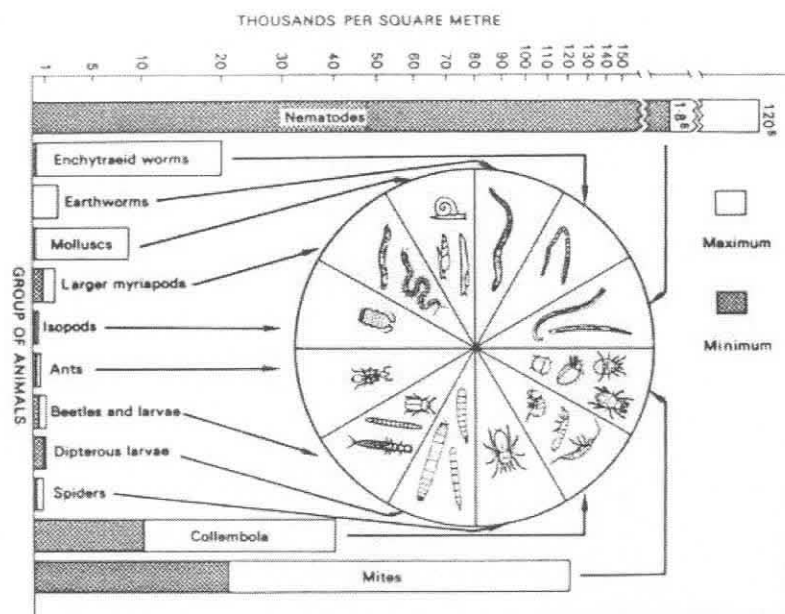
Fig. 1: Major groups of soil invertebrates and range of population densities typical of a cool, temperate grassland in Europe. (From Kevan 1965).

This paper considers invertebrate populations and activities in the context of the soil environment (which is both a constraint on, and an expression of, their activities), effects on soil processes including activities which indirectly influence N cycling, and the effects of agricultural practices on soil invertebrate populations.

FUNCTIONAL ATTRIBUTES OF SOIL FAUNA AND THEIR INTERACTIONS WITH MICROORGANISMS

Soil organisms can be classified by width into microflora and micro–, meso– and macro–fauna (Fig. 2). The definition of these categories is arbitrary since some groups have overlapping size distributions and some of the larger invertebrates could be classified as mesofauna in early developmental stages. Most Classes or higher taxa of soil organisms include saprotrophs (organisms utilizing dead organic matter), necrotrophs (organisms killing their food resource), biotrophs (exploiting living organisms), and non–specialised organisms which exploit more than one of these trophic modes. These, and finer, trophic distinctions have been defined down to species level for well–studied groups such as protozoa (Clarholm 1984), nematodes (Freckman 1982), mites and collembola (Petersen and Luxton 1982; Visser 1985) and earthworms (Lee 1985). None the less, there are a whole variety of properties related to size and mass which characterise the functional attributes of decomposer communities (Cousins 1980): mass is negatively correlated with the intrinsic reproductive rate (r_m) and positively correlated with generation times of organisms (Heron 1972): production and metabolic rates of soil invertebrates are also a positive function of mass (Petersen and Luxton 1982).

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In addition, size and mass determine the extent to which the activities of the animals are constrained by soil structure or modify their habitat through burrowing and feeding activities (Anderson 1987).
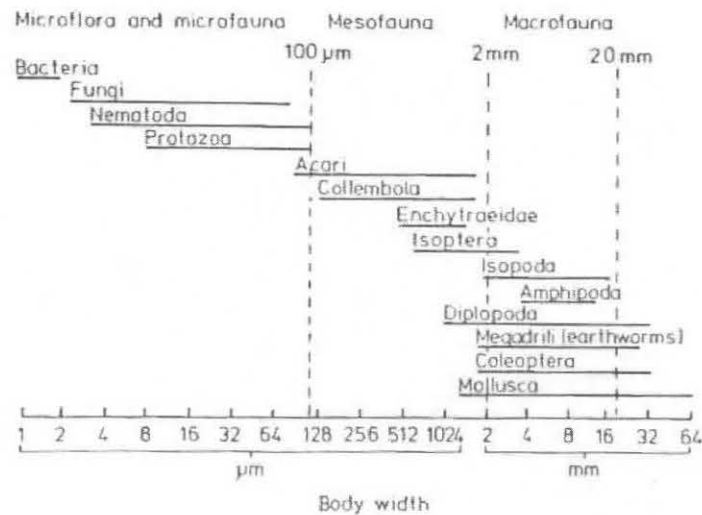

Fig. 2: Classification of soil organisms by thallus or body width. (After Swift et al. 1979).

Microfauna

The microfauna (mainly nematodes and protozoa) occupy water-filled soil pores and water films in the soil at similar scales to fungi and bacteria (root-feeding nematodes are not considered here). Microbial generation times in soil are in the order of hours, days or even longer according to carbon availability (Chapman and Gray 1985; Clarholm 1985) with higher rates in the rhizosphere than bulk soil as a consequence of root exudates (Bowen and Theodorou 1979).

Nematodes and protozoa feeding on bacteria and fungi utilize higher quality food resources in microbial protoplasm than the plant structural materials exploited by saprotrophic microorganisms; consequently their generation times can be faster than those of their microbial prey which are limited by carbon and nutrient availability from higher plant materials (Ingham et al. 1985). Bacterial- and fungal- feeding nematodes and protozoa are thus able to respond rapidly to microbial growth, exploit local food resources and then encyst until the next pulse of activity (Clarholm 1984).

The distribution of microbial cells within soil pores of different sizes, and the continuity of water in capillary spaces connecting pores, impose constraints on the capability of these microfauna to exploit their microbial food resources (Elliott et al. 1980; Anderson 1987). Darbyshire et al. (1985)

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measured pore-size distribution in a clay soil under arable cultivation and recorded a modal pore diameter frequency of $10 \mu m$ diameter to a depth of 25cm. Mobility of a major proportion of nematode populations is limited by pores below $\underline{c}$. $20 \mu m$ with optimum conditions of pore and particle sizes at least an order of magnitude larger (Wallace 1962) but some flagellates and naked amoebae can penetrate pores as small as $2 \mu m$ diameter (Clarholm 1984).

There is some evidence that predation by protozoa can decrease bacterial population densities both in the rhizosphere of crop plants (Darbyshire and Greaves 1967) and in bulk soil. Protozoa can consume 10^3 to 10^5 bacterial cells per division (Clarholm 1985) and nematodes consume in the order of 2 to 72×10^5 bacteria/nematode/day (Ingham et al. 1985). Stout and Heal (1967) calculated that, in a temperate arable soil, protozoa could consume between 150 and 900g bacteria/m^2/y equivalent to between 15 and 85 times the standing crop of bacteria. Reciprocal changes in bacteria and protozoa numbers have been detected in a semi-arid grassland (Ingham et al. 1986a) and in a comparative study of tilled and no-till arable systems (Elliott et al. 1984). Schnurer et al (1986) suggest that to invoke a causal relationship between these trends it is necessary to sample soils at intervals of a few hours. Using daily enumerations Cutler et al. (1922) were able to demonstrate an inverse relationship between bacteria and amoebae in 86% of samples during the course of a year. Recent laboratory studies show both increases and decreases in bacterial and fungal densities as a consequence of feeding by nematodes and protozoa (Ingham et al. 1985) but the extent to which these interactions are density dependent and, in the strict sense, regulate microbial populations has not been demonstrated.

Mesofauna

Collembola and mites are the most abundant mesofauna in temperate grasslands and arable soils where they mainly inhabit surface litter and air-filled macropores down to $\underline{c}$. $100 \mu m$ diameter. Many species are fungal-feeders and laboratory studies have shown that they have the potential to affect the distribution, growth and activities of saprotrophic fungi (Seastedt 1984; Visser 1985), adversely affect plant growth by grazing on vesicular-arbuscular mycorrhiza (Warnock et al. 1982), and reduce the inoculum potential of root-infecting pathogens such as Pythium, Fusarium and Rhizoctonia on seedlings. Ulber (1983) found that the proportion of sugarbeet seedlings lethally infected by Pythium ultimum was reduced from 92% to 9% in sterile soils inoculated with the collembola Folsomia firmentaria. However, another collembola, Onychiurus armatus, is one of a group of soil invertebrates which can cause economic damage to sugarbeet crops by feeding on the roots of seedlings causing death by damage or through enhancing susceptibility to pathogens (Brown 1985). Attempts to quantify these types of counterbalancing effects influencing the growth of field crops have proved intractable for two main reasons. Firstly, it is not yet possible to relate the plant response to the amount of the total microbial biomass, or root mass, influenced by invertebrate feeding. Secondly, the experimental removal of key

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species in the community using biocides may result in changes in the activities of other organisms in the community.

It has been established for some time that collembola populations may increase following applications of DDT, aldrin and some carbamate and organophosphorus pesticides as a consequence of reduced predation by mesostigmatid mites which are more susceptible to these agrochemicals than collembola (Edwards and Lofty 1969). More recently, complex indirect effects of biocides have been shown by Santos et al. (1981) in a desert system where the elimination of nematophagous tydaeid mites in litter resulted in an increase in populations of nematodes feeding on baccteria and yeast, and a decrease in litter decomposition rates as a consequence of reduced microbial activity. Similar studies by Ingham et al (1986b) using a number of selective biocides on the total soil biota of a semi—arid grassland produced complex compensatory changes in the soil biota which are difficult to interpret. The complexity and variability of these responses bring into question whether current biocides can be used to unravel the functional links in more complex communities where more species and trophic links are operating.

As yet there is little evidence that mesofauna feeding activities significantly affect the distribution and abundance of bacteria and fungi in grassland and arable soils.

Macrofauna

The soil macrofauna involved in litter decomposition (millipedes, isopods, earthworms, termites, etc.) are large enough to modify soil structure and the distribution of organic matter on and within the soil through their feeding and burrowing activities. The earthworms and termites are the best documented groups in terms of these ecological roles and their effects on soils.

Earthworms

Earthworm casting rates range from 75 to 250 t/ha/y in temperate soils (Edwards and Lofty 1972) to 1200 t/ha/y in a tropical savanna where geophagous species were estimated to ingest 5—36 times their body weight per day (Lavelle 1978). Even higher casting rates for tropical earthworms, up to 2600 t/ha/y, are reported by Edwards and Lofty (1972) but the extrapolation of short—term studies to an annual estimate is often the basis of these high values.

Litter—feeding species have low assimilation efficiencies (in the order of 10%) and it has been calculated in a number of studies that moderate population densities of earthworms turnover the annual carbon inputs to the system several times a year (Lee 1983). This intimate mixing of organic and mineral material has been found in pot experiments to increase stabilized, clay—bound carbon by up to 17%, depending on soil type (Shaw and Pawluk 1986), though field evidence of this phenomenon is lacking. Many field studies have,

however, reported that earthworm-worked soils generally have higher porosity, increased field water-holding capacity, 2 to 10 times higher water infiltration rates, more water-stable aggregates, and increased availability of plant nutrients than soils where worms are scarce or absent (Lee 1985).

But the causal relationship between these properties and earthworm activities should not be assumed because of the covariance between earthworm populations and other plant and soil parameters considered earlier. Nordstrom and Rundgren (1973) could find no significant correlation between soil porosity and earthworm biomass in 20 forest and pasture sites in Sweden and concluded that the turnover of roots had a major effect on pore space. On the other hand close relationships between burrow densities and infiltration rates have been shown in a number of temperate and tropical studies. Ehlers (1975), for example, found that infiltration rates, which were five times higher in a zero-till cornfield than normally tilled plots, were related to earthworm burrow densities. Aina (1984) recorded infiltration rates of 82 L/h and 6 L/h respectively for an old bush-fallow and a cleared site cultivated under cassava for 12 years. In the bush-fallow, earthworm channels (1 to 10 mm diameter with a modal frequency of 3 to 5 mm) averaged $220/m^2$ compared with the arable plot where channels (mainly in a 1 to 3 mm diameter range) averaged $36/m^2$.

The clearest demonstration of the agronomic importance of these effects is where exotic species of earthworms have been introduced to soils where earthworms are absent or have different feeding activities, or where earthworms are eliminated by agrochemicals.

Earthworm introductions have been carried out in a number of geographic regions (Ghilarov and Perel 1984). In New Zealand production of some pastures increased initially by more than 70% when introduced earthworms (Lumbricus rubellus and Aporrectodea caliginosa) mobilized nutrients accumulated in grass litter mats (Stockdill 1982). The nutrient flush subsequently declined but yield enhancement remained at c. 25–30% as a consequence of these introductions (Syers and Springett 1984).

Springett (1985) documented the further effects of introducing Aporrectodea longa, which is a deep-burrowing earthworm, into pastures where populations of surface active species (A. caliginosa, A. trapezoides and Lumbricus rubellus) were already established. Prior to the introduction of A. longa, the top 5–7 cm of the soil was well structured with no turf mat but roots only penetrated to the depth of this surface horizon and were susceptible to rotting when the soils were water-logged over winter. After 18 months the patches where A. longa had been introduced doubled total porosity below 10 cm depth, infiltration rates also doubled, rooting depth increased and there was a small increase in pasture production. Similar effects on soil properties followed the introduction of mixed populations of surface-active and deep-burrowing lumbricids into pastures on reclaimed polder soils in the Netherlands (Hoogerkamp et al. 1983). After 8 years the inoculation sites

could be seen in aerial photographs as patches of enhanced sward growth, infiltration increased to 120 to 140 times that of control plots and gleying of the profile was reduced.

Edwards and Lofty (1980) used a fumigant (DD) to eliminate earthworms from soil used for continuous cultivation of cereals for 6 years using direct-drilling. Some soils were inoculated with deep-burrowing earthworm species (A. longa and L. terrestris) or shallow-burrowing species (A. caliginosa and A. chlorotica), with unfumigated soils and fumigated soils without added worms as controls. Barley production was similar for the different treatments but root mass and rooting depth were increased in the worm treatments. Earlier experiments by Edwards and Lofty (1978) had shown increased barley shoot and root development in large, undisturbed soil cores to which mixed populations of soil arthropods had been added. Very large increases in cereal yields have been attributed to the activities of earthworm populations by Atlavinyte and colleagues in the USSR (Lee 1985) but details of field studies are not available and the basis of the improved fertility cannot be established.

Dung beetles

The burial of dung by beetles is analogous to the role of earthworms in producing a surface water sink at the site of deposition, relocating the dung in an environment more conducive to microbial decomposition and reducing the period of contaminated herbage avoidance by stock. McKinney and Morley (1975) calculated, however, that at 2 cows/ha in Australia about 4% of the pasture would be covered by dung and hence this represents a maximum ameliorative effect of dung beetles assuming that they were the sole agents of dung removal. Similarly, the zone of enhanced herbage growth at the site of dung burial was less than 8-15% of the total area giving an enhanced herbage production of 1-3%; and agronomically insignificant contribution to pastures receiving regular applications of fertilizer.

Termites

Termites affect soil properties and processes through four main types of activity (summarised from Wood 1987).
1. Physical modification of soil profiles through the construction of mounds, sheeting, foraging runways and infilling of large food masses.
2. Changes in soil texture involving the selection of clay fractions from sub-soil for constructions.
3. Changes in the nature and distribution of organic matter and plant nutrients through litter brought into the nest, which is more or less completely catabolised (digestion and microbial activity) in situ and the composition of termite-worked soil which has higher CEC and exchangeable bases than the surrounding soil.
4. Construction of subterranean galleries which affect drainage and moisture regimes in the soil.

The quantitative significance of these processes can only be illustrated here. In some African savannas up to 10t/ha/y of soil is brought to the surface by termites (mostly Macrotermitinae) which can remove 60% of wood and grass litter production (Collins 1983). Wielemaker (1984) reports that even on intensively cultivated, 20% slopes in Kenya intense termite activities virtually eliminated surface runoff and erosion because of the stability and porosity of the soil. In many regions of Africa and India, surface mounds, which can represent considerable concentrations of available plant nutrients in the system, are often used for soil amelioration by farmers. Lal (1987) cites examples of cultural practices in Tanzania where mounds, containing as much as 3.5% $CaCO_3$, contributed the equivalent of 11 t/ha of lime, but in Zaire mounds on clay soil had lower fertility than surrounding soil and were an impediment to mechanised farm operations. The agronomic significance of termites is clearly determined by a fine balance between their beneficial effects on soil conservation and fertility, and their pest status which can vary from year to year according to climatic conditions.

Having established the many ways and spatiotemporal scales at which soil invertebrates affect soil processes their net contributions to soil N fluxes will be considered next.

EFFECTS OF INVERTEBRATES ON NITROGEN FLUXES

Soil invertebrates contribute both directly and indirectly to N fluxes. The direct contributions are the mobilization of N through trophic transfers in food webs from trophic level n to level $n+1$ (feeding, excretion) and turnover of tissue production. The indirect effects involve feedbacks to the controls over the activities of organisms of lower trophic levels, e.g. predators altering prey/microbial interactions and the activities of meso- and macro-fauna changing the physicochemical conditions of microbial habitats.

Direct effects

Estimates of N fluxes through the soil biota can be made for systems where sufficient data are available on soil invertebrate and microbial populations. Information on feeding rates, assimilation, excretion and other physiological constants are available in the literature and can be applied according to defined, functional groups of organisms. There are few detailed studies of N fluxes in grassland or arable systems using this approach.

System budgets

Hunt et al. (1987) investigated the soil N transformations in a shortgrass prairie in the USA, which will be functionally similar to many semi-arid rangelands. They used a food-web model which involved 8 trophic levels and 12 faunal groups with resource inputs separated into resistant and labile fractions to represent the widely divergent decomposition rates of plant and soil organic matter fractions. Groups excluded from the model,

because of their low biomass on this site, included ciliates, earthworms, termites and insect larvae. Bacteria were estimated to mineralise the most N ($4.5g/m^2/y$ followed by the invertebrates ($2.9g/m^2/y$) and fungi ($0.3g/m^2/y$). In this system the fauna mediated about 38% of the 77 kg/ha annual flux of mineral N with bacterial—feeding amoebae and nematodes accounting for over 84% of the N mineralized by the fauna.

At the other extreme, detailed N budgets have been drawn up for four cropping systems within the Swedish Ecology of Arable Lands Programme (Rosswall and Paustian 1984): a lucerne ley without fertilizer, a meadow fescue ley receiving 200 kg N/ha/y, barley receiving 120 kg N/ha/y and barley without fertilizer N. Sampled fauna were divided into trophic groups and metabolic constants, and transfer efficiencies between trophic levels, were then applied from the literature. The N budget for barley without fertilizer is shown in Fig. 3. It was concluded that the soil fauna were important in releasing mineral N through consumption of microbial biomass with a low C/N ratio. Only the protozoa and nematode faunas were estimated to excrete significant amounts of ammonium. The direct contribution of the fauna to N
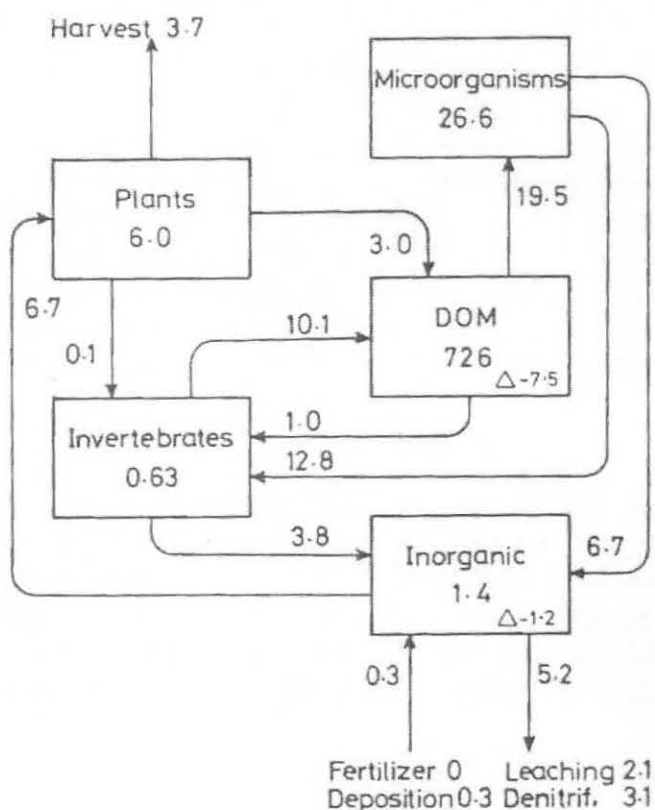
Fig. 3: Summarized N budget for an unfertilized annual barley crop in Sweden. Compartment values are in g/m^2 and represent peak standing crop for plants and mean annual values for all others. Delta symbols indicate net changes, otherwise compartments are assumed to be in steady state. All flows expressed as $g/m^2/y$. DOM = Dead organic matter. (After Rosswall and Paustian 1984).

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mineralization was highest in the leys (c. 42–50 kg/ha/y) and lowest in the barley plots (c. 38–40 kg/ha/y). However the proportion of total mineralization attributed to the fauna was 31–36% in the barley plots compared with 19–20% in the leys. Earthworm populations in the leys, with a biomass of 50 kg d.w./ha, were considered to have an insignificant contribution to N fluxes but this probably underestimated their roles in the system.

Nitrogen mobilization by earthworms

Lee (1983) calculated that an earthworm biomass of 5 g d.w./m^2 (50 kg/ha), represents a turnover of about 1 gN/m^2/y, assuming a production to biomass quotient of 2–5 and tissue comprising 10–12.5% N. With excretion contributing a further 1.8 gN/m^2/y the total flux through worm tissues is equivalent to 28 kgN/ha/y. For the most densely populated New Zealand pastures with a worm biomass of 450 kg d.w./ha the total could be in the order of 275 kgN/ha. The total N flux mediated by the worms will be much higher because a major proportion of the ingested N is not assimilated. Syers et al. (1979) found that surface casting in a New Zealand pasture, by a (undefined) population of L. rubellus and A. caliginosa, amounted to 33 t/ha/y and contained 73% (132 kg N) of the total N content of litter removed by the worms. Of the total N in the casts only 3.5 kg/ha was in mineralized forms, a smaller mineral N pool than in control litter during the study period, and they concluded that casting was not an agronomically significant N flux pathway in these pastures.

Andersen (1983) investigated N turnover by earthworms in arable plots in the Netherlands receiving inputs of 120 kgN/ha/y as compound fertilizer plus varying treatments of up to 400 t/ha/y of slurry or farmyard manure. Earthworm biomass was 30 g(fresh wt.)/m^2 or less in all plots (Table 1), equivalent to about 5 g d.w./m^2, assuming 16% dry matter (Lakhani and Satchell 1970). Production estimates, derived using a number of different methods, resulted in P/B quotients of 2–4. The results, summarised in Table 1, show that the worms consumed 3–4 t/ha/y of organic matter and turned over 9.5–13.3 kg N/ha/y. While this theoretically represents only 5–6% of the N flux to plants in Andersen's plots, if the figures for the control plots receiving inorganic fertilizer are extrapolated to the Swedish study considered above then a biomass of 50 g/m^2 would mediate a flux of about 95 kg N/ha/y; or about twice the estimate of Lee (1983). Such extrapolation is not really justified but it does illustrate the difficulty of determining N turnover through populations of accessible invertebrates such as worms let alone the problems of estimating populations, processes and N fluxes for mesofauna and microfauna.

Termites and N fluxes

The pathways and processes of N fluxes mediated by termites are complex and will not be considered here (see Wood and Sands 1977; Collins 1983). Termite populations do not turnover N in situ in the same way as earthworms

Table 1: Earthworm populations; feeding activities and N turnover in arable plots in the Netherlands receiving annual applications of compound fertilizer (control), farmyard manure (FYM) or slurry (SL). (Data from Andersen 1983).

	Control	100t/ha FYM	100t/ha SL
Application (kg/ha)			
inorganic N	120	147	266
organic N		412	187
Plant uptake of N (kg/ha)	189	211	230
N turnover by worms (kg/ha)	9.5	13.3	12.0
N flux via worms as % of plant uptake	5	6	5
Worm density (no./m^2)	123	219	237
Worm biomass (g f.w./m^2)	23.6	29.4	26.8
Consumption of organic matter (kg/ha/y)	2 950	4 040	3 700

but transport nutrients to their nests, to varying extents, from which N is mainly returned to the system through predation of workers and alates. Termite biomass generally ranges 0.2–5.0 g d.w./m^2, sometimes as high as 20g/m^2, and N returned to the system through biomass turnover is normally 1-25 kg/ha (Lee 1983). Collins (1983) has calculated for Macrotermes in Kenya and Nigeria that the annual turnover of N is c. 7.6 and 75 kg N/ha/y respectively. These estimates indicate the potential significance of litter–feeding termites in savannas where N turnover between plants and soil is 20–40 kg/ha/y under dry regimes and up to 80 kg N/ha/y with increasing rainfall and herbivory (Bate 1981).

It is important to recognise that the N fluxes calculated in these budgets represent turnover by the biota and not necessarily N mineralization. Excretory ammonium–N is immediately available to plants but N organic excretory products (urea, uric acid and amino acids) and dead tissues must be reutilized and recycled many times for complete ammonification. Hence the mineral N flux to plants mediated by fauna will usually be much less than N turnover through earthworm populations. These estimates of the role of fauna in soil N fluxes are therefore based on necessarily simplistic models of N transformations from tissue N to excretory ammonium with no quantification of the complexities of N recycling in the biota. It is also assumed that the fauna have no indirect effects on microbial N flux pathways. An alternative approach to investigating animal–mediated N fluxes to plants is to set up exclusion experiments with animals which are assumed to have predominantly direct effects on N mineralization. Only nematodes and protozoa, which have

fast turnover rates for living and dead tissues, feed on fungi and bacteria, and do not affect soil structure, meet these specifications. However, such defined experiments can only be set up in the laboratory.

Microfauna mediated N uptake by plants

Enhanced N uptake by the grass _Bouteloua gracilis_ occurred in the presence of bacteriophagous protozoa (Elliott et al. 1979; Ingham et al. 1985) or with fungal-feeding nematodes (Ingham et al. 1985). Also, Clarholm (1984) found wheat plants grown in autoclaved (but unleached) arable soil had 60% higher mass and N content when inoculated with protozoa and a natural complement of soil bacteria than when inoculated with bacteria alone (Table 2). A lower shoot/root ratio was found in the presence of protozoa suggesting an improved nutrient supply to the roots. The mechanism put forward by Clarholm (1985) to account for the enhanced N mineralization is that N immobilized in the rhizosphere, as a consequence of bacterial stimulation by root exudates, is mobilized as excretory ammonium by protozoa. It is debatable, however, that this phenomenon is significant in mediating a significant proportion of the N uptake by arable crops since these require low rooting densities to efficiently exploit a mobile ion such as nitrate which is the main form of N taken up under field conditions (Robinson and Rorison 1983).

Table 2: Dry weights and N contents of wheat plants grown for 6 weeks in sterilized soil reinoculated with bacteria alone or bacteria plus protozoa. Values are expressed as mg per experimental chamber containing 3 plants. (From Clarholm 1984).

Component		Bacteria alone	Bacteria + Protozoa
Dry weight	shoots	116	213
	roots	65	113
	total plant	181	326
N content	shoots	3.92	4.39
	roots	0.93	1.41
	total plant	4.85	5.80
N content	planted seeds	3.24	3.24
N mineralized from soil (plant N – seed N)		1.61	2.56

Indirect affects

Indirect effects of invertebrates on N fluxes from dead organic matter to

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root uptake by plants include: the removal of litter N pools from the system; influences on litter decomposition rates by transport to more or less favourable environments for decomposition; alteration of the conditions for root growth and activity; and rhizosphere effects on pathogens and mycorrhizas. Springett and Syers (1979) also mention 'plant growth substances' in earthworm casts; a hypothesis put forward by earlier workers to account for aberrant root growth patterns in grass seedlings. The present discussion is restricted to indirect effects on microbial processes of N mineralization and N availability to plants.

Indirect effects are difficult to demonstrate and even more difficult to quantify, particularly for micro-fauna, except by the removal or addition of key animals to the system and monitoring the response. Salawu and Estey (1979), for example, carried out pot experiments in which soybeans were grown in sterile soil alone, in soil inoculated with spores of Glomus (a VA mycorrhizal fungus), and Glomus spores plus fungal-feeding nematodes (Aphelenchus avenae). After 45 days the top-growth of plants treated with Glomus alone was up to 40% higher than for treatments with Glomus and nematodes; but there was only a 12.9% difference between control plants without the mycorrhiza and treatments with nematodes and mycorrhiza. It was also found that the simultaneous addition of both nematode and VA fungus resulted in the formation of only 3 nodules/plant compared with 24 nodules/plant for the treatment with Glomus alone; a difference attributed to the indirect affects of the nematodes on P uptake by the soybean plants.

It has proved difficult to carry out comparable manipulations of microfauna in the field. Ingham et al (1986b) used pulse teatments of selective biocides in a semi-arid grassland to reduce populations of bacteria (streptomycin), fungi including VA mycorrhizas (captan and PCNB), nematodes (carbofuran) and microarthropods (cygon), and monitored responses for 7 months after biocide application. Overall, groups were reduced rather than eliminated by the biocides and responses were complex. But the results are of particular interest since they show that the community did not return to the original composition within 7 months but, after an initial flush of mineral N, no further changes in mineral N fluxes were observed because of compensatory flux pathways operating within the food web.

The effects of macrofauna on microbial populations are best documented for base-rich soils which are intensively worked by earthworms. Bhatnager (1975) estimated that 40% of aerobic, non-symbiotic N_2-fixing bacteria, 13% of anaerobic N_2-fixers and 16% of denitrifying bacteria in the total soil volume were located in a narrow zone of a few millimetres depth around earthworm burrows in a French pasture. The casts contained fewer fungal propagules and denitrifying bacteria, higher counts of total bacteria and more hemicellulolytic, amylolytic and nitrifying bacteria than unworked soil (Loquet et al. 1977).

When casts are first voided mineral N predominates as ammonium but nitrification progresses rapidly at field temperatures under which the worms

are active (Syers et al. 1979). The conditions for microbial growth in the casts are largely determined by selective feeding by the worms on plant materials and soil organic matter, and will therefore be determined by the ecology of different species. Ingestion of high quality food will produce casts with higher mineral N and available carbohydrate than the surrounding soils (Syers et al. 1979). As a consequence of enhanced heterotrophic microbial activity in the casts oxygen is depleted leading to the development of anaerobic conditions in which denitrification can take place (Svensson et al. 1986). Casts of L. terrestris fed on lucerne (Medicago sativa) were shown by Svensson et al. (1986) to consistently maintain higher rates of nitrous oxide production (using the acetylene inhibition assay) than soil controls. The maximum rates of denitrification in the casts, approaching 0.2 mgN/g soil, cannot be extrapolated from these laboratory studies to the field but these workers suggest that the phenomenon may contribute to the high spatial variability of denitrification rates observed in field studies. This is supported by a preliminary results (P. Elliott, D. Knight and J.M. Anderson, unpublished data) for a permanent pasture in the UK where mean (+SE) denitrification rates in earthworm casts, during a spring period of low rainfall, were 0.380 ± 0.24 mgN/g soil compared with 0.03 ± 0.27 mgN/g from paired soil cores. It is of interest in this respect that large-earthworm casts are very similar in size and texture to the soil aggregates which Tiedje et al (1984) have shown to form anaerobic cores and constitute sites of denitrification during nitrate flushes in a well-drained silty loam under continuous arable cultivation.

Surface runoff represents another pathway of N loss which is influenced by termites and earthworms. Sharpley et al (1979) treated permanent pasture with carbaryl and found that the elimination of earthworms doubled surface runoff. This was attributed to a three fold reduction in infiltration rate in the absence of surface casting by earthworms which maintain the openings of the burrows to the soil surface. The decreased infiltration in the absence of the worms resulted in greater net losses of dissolved inorganic N (13.8 kg/ha/y) in the treated plots than in the untreated grassland with casts present (2.2 kgN/ha/y).

Soil fauna clearly have a whole spectrum of effects which affect soil fertility and plant growth in agricultural systems. It is appropriate, therefore, to consider the effects of agricultural management practices on their populations.

INVERTEBRATE POPULATIONS AND MANAGEMENT PRACTICES

The two main determinants of species diversity and population densities of soil invertebrates excluding climate, are the quality and quantity of detritus inputs to the system (Heal and Dighton 1985), and the stability and complexity of soil and litter habitats (Anderson 1978). The two factors interact through the regulatory role of resource quality on litter decomposition rates (Swift et al. 1979; Heal and Dighton 1985). As resource

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quality increases the accumulated litter and cellular soil organic matter pools decrease as a consequence of faster decomposition. Hence microhabitat complexity and diversity of associated species are also likely to decline. Conversely, populations of larger soil invertebrates and their contribution to total fauna biomass tend to increase as some function of increased N turnover in natural systems (Heal and Dighton 1985).

Earthworms and other macrofauna consume soil and organic matter forming a microhabitat for smaller invertebrates, and Yeates (1981) has suggested that their feeding activities may constitute an incidental but density—dependent source of mortality for soil nematodes. In natural systems these patterns of community structure are to some extent predictable because of the integration of plant production, litter quality, soil organic matter pools and N cycling in relation to parent soil types and climate. But in agricultural systems factors affecting the soil invertebrate community (Fig. 4) may be imposed independently or in combinations which have interactive effects which are poorly understood.

Fig. 4: Ecological effects of agricultural practice on soil fauna populations. (From Edwards and Lofty 1969).

Pesticides

Pesticide effects are particularly complex because of differences in exposure and sensitivity of non—target species (Edwards and Lofty 1969; Smith et al. 1980; and other reviews in Dindal 1980), changes in soil conditions influencing the inactivation or degradation of the pesticide (McColl 1984) and trophic interactions in the community (Parker et al. 1984; Ingham et al. 1986b) which are considered below. Herbicides also give complex effects by

providing a pulsed input of plant material to the soil which, for example, can produce a short term increase in earthworm populations but a long term decline through sward removal (Edwards and Brown 1982). The organophosphorus and carbamate pesticides have transient effects on nematodes and microarthropods but populations of earthworms, such as L. terrestris, may take longer to recover because of lower reproductive rates and colonising abilities than smaller invertebrates. Standard spraying regimes of the fungicide benomyl can significantly reduce earthworm numbers and activity (Stringer and Wright 1973; Keogh and Whitehead 1975) and some insecticides are also extremely toxic to earthworms. After three years spraying pasture in the UK with the insecticide phorate (3.3 kg/ha/month) earthworm populations were eliminated with consequent changes in soil physical properties (Clements 1978). In comparison with the untreated plots, infiltration rates and hydraulic conductivity were reduced by c. 93% and bulk density increased by up to 17%; none-the-less, herbage yield increased 40% as a consequence of controlling root-feeding beetle larvae.

Perfect et al. (1979) found that spraying cowpea with DDT over a 4-year period doubled grain yield in a Nigerian bush-fallow rotation with no fertilizer inputs. But the decline in yield over the cropping period, as is usual in these systems, was faster in the treated plots and was particularly marked in a subsequent maize crop. The effect was not attributable to greater nutrient depletion in the more heavily cropped plots. It was concluded that differences in soil fertility arose through supression of earthworm effects on soil properties at concentrations which had little effect on population densities (Perfect et al. 1979). Edwards and Thompson (1973) concluded that in temperate, cultivated soils the overall effects of tillage have greater long-term impact on soil invertebrate communities than modern pesticides.

Other management practices

In temperate grasslands, old leys and permanent pastures have the highest population densities of most invertebrate groups. Microclimatic conditions and soil surface microhabitats associated with grass cover, litter and the root mats favour microarthropods such as mites and collembola which can have population densities as high as $300000/m^2$ (Curry 1969). Stocking densities of cattle or sheep influence the quantity, quality (dung rather than litter) and distribution of resource inputs to the soil, herbage cover and soil porosity through trampling. Hutchinson and King (1980) found that sheep stocking density (10, 20 and 30 animals/ha) affected the abundance and biomass of all invertebrates. But while numbers of small animals (mites, collembola, enchyraeid worms, nematodes, etc.) were inversely related to sheep density many of the larger invertebrates, such as earthworms and scarabeid larvae, reached peak abundance under the intermediate stocking level.

Organic manures (such as slurry and farm-yard manure), and inorganic fertilizers increase soil fauna populations through increased pasture growth and higher residue quality. Cotton and Curry (1980) recorded worm populations

of 400–500/m^2 (100–200g f.w./m^2) in grassland fertilized with slurry while applications of superphosphate with lime in the clover–rich pastures of New Zealand have resulted in very large lumbricid populations of more than 1000/m^2 (c. 300 g f.w./m^2) (Lee 1985). Comparable worm population densities of 800/m^2 have been recorded in northern England for a hay meadow dressed with fertilizer and farmyard manure to a total of 118, 42 and 111 kg/ha/y N, P and K respectively. Soil pH and manure applications were positively correlated with earthworm populations in this study but enchytraeid populations, which are highest in acid soils, were negatively correlated with earthworm biomass.

Drainage of soils under permanent, fertilized grassland (Gilbey 1985) or forage crops (Carter et al. 1982) increased earthworm populations but interpretation is complicated by improved soil environmental conditions and plant production.

When grassland is ploughed and maintained under arable cultivation the number of invertebrate species and population densities are usually drastically reduced. The changed soil environment and disturbance selects for small species with high reproductive rates and against larger invertebrates, such as earthworms, with a life cycle of more than a year (Edwards and Lofty 1969). The restructured community may include higher proportions of insect pests (Edwards and Lofty 1969). Andren and Lagerlof (1980) observed major differences in the composition of microarthropod communities in a 5 year-old ley compared to the first and second barley/ley rotations. Collembola were dominant (c. 60000/m^2) in the maintained ley but reduced to a similar density to mites in the first crop rotation and to only 10000/m^2 in the second rotation where small, fungal–feeding prostigmatid mites (Tarsonemoidae) were most abundant (c. 35000/m^2). Contrary to the observation by Ferris (1982) that plant parasitic nematodes, and to some extent bacterial feeders (Sohlenius and Bostrom 1986) show a proportional increase in arable systems, Andren and Lagerlof (1980) found that all trophic groups of nematodes were reduced by c. 50% from 8 x 10^6/m^2 in the ley to about 2 x 10^6/m^2 in the second crop rotation.

Low (1972) compared earthworm populations in old grassland with grassland cultivated for three years and with fields tilled for 25 years on the same soil series. After three year's cultivation the worm populations were half those in the grassland and reduced to about 14% over longer periods of cultivation.

In the short term, shallow tillage is much less damaging to worm populations than deep ploughing; particularly for deep–burrowing species (Edwards 1983). But in the long term the loss of surface litter and reduced organic matter content of soils is mainly responsible for the decline in worm populations in tilled soils (Lee 1985). Minimum tillage practices, through reduced soil disturbance and increased weed and crop residue inputs, generally show higher populations of nematodes (Stinner and Crossley 1982), microarthropods (Edwards and Lofty 1969) and earthworms (Lee 1985) than

conventionally tilled systems. Edwards and Lofty (1982) recorded a thirty-fold increase in worm populations after eight years of direct drilling fields which had previously been ploughed.

DISCUSSION

Natural grassland and forest ecosystems develop towards a state of dynamic equilibrium between organic N inputs to the soil and mineral N uptake by roots. Once this state is reached plant communities with similar net primary production can exhibit significant differences in the size and turnover of different nutrient pools within the system (Cole and Rapp 1981) and in the structure and functioning of soil organism communities. In functional terms, therefore, the various animal and microbial processes will equilibrate with the availability of N in the system and hence the various pathways involved in N mineralization though faunal effects may not be of direct consequence for plant production under 'steady state' conditions. Similarly, water infiltration rates are usually high, and soil erosion and surface—water runoff usually low, under undisturbed vegetation cover associated with faunal communities which are very different in structure and functioning.

If, however, some component of the system is changed, such as quality or quantity of soil organic matter and nutrient inputs, climate or soil parameters (including the introduction or removal of soil fauna), then the whole functioning of the community may shift to a new equilibrium (Anderson 1987). During the transitional phase soil fauna may act as driving variables determining both the rate of change and the new equilibrium state. Once the new state is reached it maintains some degree of resilience to small and frequent, or severe and infrequent perturbations. For example, Anderson et al. (1985) established a series of lysimeters in an oak woodland with and without a small biomass of soil macrofauna (about 3.7 g d.w./m^2 of millipedes, woodlice and surface—living earthworms) and with and without tree roots to act as water and nutrient sinks. After a year the humus form and the mineral N fluxes were different in the four treatments with enhanced total mineral N losses from the macrofauna treatments of c. 12 kg/ha over the summer/autumn period and reduced mineral N losses over winter/spring. But when the soil fauna were killed by a single, large application of carbofuran there were negligible changes in the N losses from experimental soils over a period of months indicating that the functional attributes of the system were the consequence of indirect effects of fauna on soil properties and processes. Similarly, the introduction of exotic earthworms into New Zealand pastures caused a large initial increase in herbage production, associated with the mobilization of nutrients from accumulated litter. Thereafter, pasture production settled down to an improved yield as a consequence of changes in soil conditions for root growth.

When continuous vegetation cover is replaced by intensive arable cropping the dynamic balance is disturbed and production occurs in cohorts of crops

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sustained by pulsed inputs of fertilizers. Tillage, pesticides and fertilizers to maintain production in this non-equilibrium state not only override faunal processes but also further reduce and obscure their contribution to soil fertility. But when the system employs residue conservation, organic manures and/or minimum-till cultivation, the soil biological processes are more evident. Under these conditions faunal processes could have an impact on plant production if we knew how to manage them to achieve specific effects within the life span of the crop plant. The role of earthworms is better understood in this respect than most other groups; although we lack detail of their interactions with soil bacteria and fungi to appreciate their manipulative potential beyond their physical effects on soils. Far less is known about invertebrate/microbial interactions in the rhizosphere.

Whipps and Lynch (1986) have reviewed the influence of the rhizosphere on crop productivity and detail the microbial responses to changes in organic exudates from crop roots following changes in the plant environment (fertilizers, pesticides, pathogens, moisture stress, etc.). At the present time the implications of these responses for the activity of root pathogens, mycorrhizas, growth-promoting rhizobacteria, rhizobia and associative N_2-fixers is poorly understood but may have considerable agronomic potential. It is already established, however, that biological control of microbial pathogens and some root-feeding nematodes can be achieved by competitive displacement, induced resistance, predation or parasites (Baker and Cook 1974). But little is known about faunal effects which may enhance or inhibit these responses though the studies reviewed earlier show that the feeding activities of nematodes and protozoa can affect microbial populations at this scale and particularly in the rhizosphere.

In conclusion, the roles of soil fauna in N cycles are difficult to quantify because in addition to their direct contributions to N fluxes there are a wide range of indirect effects on the soil as an environment for microorganisms and plant roots. Consequently, treatments which enhance or reduce soil invertebrate activities, particularly those of macrofauna, may not be interpretable in terms of simple cause/effect relationships. It would appear that there are soils and management circumstances where these net effects on soil processes may be important. The current interest on less intensive, more organically based agriculture in Europe and N. America, and on improving and sustaining low-input agriculture in the tropics (Swift 1985), may result in stimulating the critical interdisciplinary approaches which are still needed to resolve the roles of fauna in soil processes.

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